hydes produce back reactions to carbonic acid and formic acid, which proceed in chains and therefore reduce the O_2 production considerably. With small intensities such absorption acts will not occur, since the average time between two consecutive absorption processes taking place in the same *Chph* molecule is large compared with the time used by the enzyme to reduce the peracid (time 1/50 sec.), but with rising intensity more and more chains start and finally produce saturation. These processes are, according to our viewpoint, responsible for flash saturation and for saturation with continuous illumination, the difference between them in respect to the saturation values being caused by the higher instantaneous density of light quanta in flash illumination. The following figures show the good agreement between observation and theoretical calculation. The points represent observed values, the drawn lines the results of theory.

Fig. 1 contains Warburg's results on photosynthetic oxygen production plotted against light intensity. The only point which deviates from the calculations is not very reliable, according to a remark by Warburg. Fig. 2 shows results of other authors plotted on a logarithmic scale. The data for this figure have been taken from a paper of Smith which contains Smith's own measurements and results of other observers. Deviations between theory and experiment are not greater than the possible error of the observations. Several points which correspond to measurements with very low light intensity have considerable possible errors, since according to Smith the correction necessary for respiration processes in the plant is here very large and not exact. In Fig. 3, observations on flash saturation (points) made by Emerson and Arnold are compared with the theoretical curve (solid line). The dotted line represents an empirical formula suggested by Kohen. The great reduction of the oxygen production at light saturation caused by HCN or low temperature fits very well in the theory, since every influence which lowers the velocity of the enzymatic decomposition of the peracid and peraldehyde increases the concentration of these substances and makes the starting of back reaction chains more frequent.

The proposed chemical mechanism has of course also a biological aspect. The back reactions proceeding in chains give us an understanding of how the plant protects itself against overfeeding. The plant, having no other possibilities to get rid of a surplus of food, uses the light which produces the food to destroy the excess.

There is not sufficient time to go further into details. I wish only to add that, according to the theory, not only carbonic acid and for-

mic acid are photosynthesized, but also all plant acids which are pro-
duced as intermediate products of respiration which combine with
chlorophyll in the way characteristic of acids. In this case also per-
acids and aldehydes will occur in the course of photosynthesis, and
are reduced by the enzyme. But there is one striking difference be-
tween these plant acids on the one hand and carbonic and formic
acids on the other.

The difference is that the plant acids, having a great number of $-\overset{|}{\underset{|}{C}}-H$ bonds, provide a great chance for photoxidation which again proceeds in chains. The result is that the $-\overset{|}{\underset{|}{C}}-H$ groups are partially replaced by $-\overset{|}{\underset{|}{C}}-O-OH$ groups, and these groups also give to the molecule the properties of a peracid. Consequently, a great excess of
peracids is built up if photosynthesis and photoxidation of the plant
acids take place as parallel processes. This will occur whenever the
plant contains a large concentration of plant acids and is strongly
illuminated in the presence of molecular oxygen. The plant acids are
produced and consumed at a constant rate by respiration, but since
with illumination there is an additional consumption of plant acids
by photosynthesis and photoxidation, the equilibrium concentration
is lower in the light than in the dark. The transition of the concentra-
tion of plant acids from the value in the dark to that prevailing in
light takes time. This time will be longer with a weak illumination
than with strong. Since in the transition period an excess of peracids
is present, the probability of starting chains of back reactions by
photolysis is enhanced, thereby diminishing the production of oxygen.
Weak illumination should have only a small influence, since the
enzyme is able to reduce the extra amount of peracids formed by
photoxidation before they absorb light quanta and split into radicals.
However, with strong irradiation, radicals are produced and the
number of back reaction chains should become considerable. This
explains Warburg's observation that there is a considerable induction
period in the oxygen production if a plant after a dark pause is il-
luminated with strong light, although with weak illumination this
phenomenon is not found. The induction period occurring with strong
illumination is intimately connected with the abnormal behavior of
the fluorescence of a living leaf strongly illuminated after a dark
period. This phenomenon, first observed by Kautski and studied in
more detail by R. W. Wood and myself, can be easily interpreted in

terms of the photoxidation of plant acids. Time does not permit me to discuss this point in more detail.

I hope that this survey of the problem of photosynthesis, which could touch only the main points, will leave you with the impression that, while the problem is by no means entirely solved, many features are made understandable by the application of normal physical and chemical experience, and that one is no longer forced to assume that in this biological problem processes occur which are of an entirely different character from those with which we deal in studying inorganic matter. I wish again to express my thanks to the Philosophical Society for the great honor of being invited to give this Joseph Henry lecture, and to the audience for listening with such patience to my remarks.

GENETICS.—*Hybridity as a factor in evolution.*[1]   ROBERT F. GRIGGS, George Washington University.

Of all the various factors that have been suggested as causes of evolution, hybridity looks, on first sight, the least probable. The limits within which species are cross-fertile are so narrow that there would seem to be little possibility of any such wholesale hybridization in nature as would appear to be demanded if the motive power of evolution is to be found in hybridity. In fact, the suggestion that hybridization may have been a major factor in evolution sounds to most people almost absurd.

The very idea of origin of species by hybridization involves almost a contradiction in terms. The best criterion of specific separability that can be framed is that the types in question will not interbreed. If, therefore, it is only exceptionally that hybrid intermediates between species can be obtained, how much less likely is it that new genera, families, orders, or classes could owe their origin to hybridization? The mere suggestion that even such closely related animals as dogs and cats could hybridize is too far-fetched to be considered by anyone. This being the case, we should perhaps drop the whole matter here and go no further.

Yet, since evolution by hybridization has been advocated by students whose biological contributions in other fields are respectable, it cannot be dismissed so cavalierly as that. The repute of the sponsors of the theory demands for it consideration on its merits.

In the first place, we may observe that the apparent absurdity of a scientific theory does not necessarily throw it out of court. While biology is still on a basis where nothing that does not appeal to "common sense" can command a hearing, the physical sciences have long since passed beyond that stage. Indeed, we biologists might well ponder the fact, for it is a fact, that the recent revolution in physics, with its many brilliant theoretical advances and its equally spectacular practical applications, was made possible only by the willingness of physicists to follow theories which led them to tenets quite contrary to any common sense view of the universe. Einstein's doctrines that time is not the same at the same instant in different places, or that a straight line is not the shortest distance between two points certainly cannot be fitted into any common sense ideology. The interesting thing about these seemingly nonsensical ideas of modern physics is that they seem to be true in spite of their apparent absurdity.

The point for us, however, is not whether new ideas appeal to our common sense (which is, I fear, only another name for the complex of our prejudices and preconceptions) but whether they are susceptible of objective test, observational or experimental. That is the great feature of Einstein's ideas which the layman often overlooks. They were not such wild speculations as they sound, for, along with their very enunciation went concrete suggestions for quantitative experimental tests by which they could be established or rejected. We will do well in biology if we will consider new ideas in the same spirit.

In the past we have done our science great harm by hastily accepting ideas which appealed merely to our "common sense." A very large part of the success of the theory of Natural Selection lay in the vivid appeal of the phrases "struggle for existence" and "survival of the fittest." Everybody thought he knew what the struggle for existence was and that he understood the survival of the fittest, and he straightway adopted the ideas without critically thinking about them. The unfortunate fact is that three-quarters of a century after Darwin his ideas are still as he left them, mere phrases without experimental substantiation. As a matter of fact, nothing is less understood than the struggle for existence.

The proper way for us to examine the rôle of hybridity in evolution is, therefore, to inquire, first, what was the factual basis for its enunciation, and second, how can it be examined objectively. If we discover no way of attacking the problem, we should follow our first reaction and drop it. If it should become merely a speculative football it would do biology no good. But if it can be tested by a large body of

data, experimental or otherwise, it may lead us somewhere. The question which I shall consider tonight, then, is whether any such objective approach to the idea is feasible.

Going a little further now with the negative side of the question, we may point out that the difficulty suggested of accounting for the larger groups—genera, families, orders, classes, and phyla—is not peculiar to the hybridity theory but is shared by most other theories of evolution.

It was not by accident that Darwin titled his book *The origin of species*. He supposed that he had discovered the factor responsible for the differentiation of homogeneous stocks into separate species, and he believed, or perhaps it would be more accurate to say that he hoped, that the operation of the same factor could, by something like extrapolation, account for the origin of genera, families, and larger groups.

The same might be said of Lamarck with even greater emphasis, for while the differences between species are to a certain extent due to adaptations which might, perhaps, be acquired by something like use or disuse, the characters which distinguish the great groups are very much less adaptive. For example, the aorta in birds turns to the left and in mammals to the right; the one has feathers and the other hair, and it would be very difficult to believe that either of these conditions was brought about by adaptation to environment.

As for mutation, we have plenty of experience with mutations involving superficial characters like pigmentation, but after all, a mutated cat is still a cat and we cannot imagine even so similar an animal as a puppy in a litter of kittens.

For orthogenesis the case is different, because with orthogenesis, as with creation, all things are possible. But also, orthogenesis has little more to offer in the way of circumstantial explanation than did special creation.

The fact that we cannot imagine hybridization to have played a rôle in the evolution of the higher categories of plants and animals does not, therefore, militate against the theory as heavily as might have been supposed.

Historically, the hybridity theory of evolution was propounded twenty years ago by Lotsy[2] of Leiden. Lotsy emphasizes the importance of the recombination of Mendelian factors, and in the mere reassortment of these factors sees the explanation of the evolution of

[2] Lotsy, J. P. *Evolution by means of hybridization.* M. Nijhoff. The Hague, 1916.

many species. He specifically disclaims any attempt to explain the whole of evolution. For him the biological unit is the "Jordanon" or Jordanian species, a group of completly homozygous individuals. Any heterozygosity to him is proof of hybridity. "All individuals able to produce more than one kind of gametes, e.g. gametes of different constitutions, are hybrids" (p. 28).

Lotsy considers genera and all groups of a higher order as largely figments of the human mind, with only doubtful reality in nature. But he asserts that these higher orders also originated by crossing. *"Crossing was the origin of the new classes; selection, the result of extermination by the struggle for life, the cause of their gradual extinction.* [Italics in original.] Such extinction of classes must proceed continuously until a happy meeting between two sufficiently differently constituted gametes, causes the origin of a new class." (p. 135). But "A formation of new classes is not in action at the present moment, so that it is illegitimate to claim that one who wants to explain evolution must demonstrate how such a formation of new classes goes on" (p. 136).

Nor does he believe in any progress in evolution. "Consequently the geological record gives no support to progression either, and we are perfectly justified to say that progression is a human conception and that progressive evolution does not exist" (p. 118).

Lotsy thus considers only a small fragment of the problem of biological relationship. And even within the circumscribed field which he has undertaken to elucidate he submits almost no evidence that his theory does, in fact, explain the origin of the phenomena ascribed to it. Considering the vast body of evidence which might have been marshalled for his proposition, it is very surprising that he should have contented himself with so speculative, not to say dogmatic, a treatment of the subject.

Lotsy's ideas of what amount to miraculous origins of new forms by rare chance fertilizations and his consequent disbelief in the gradual origin of families and other larger groups led him to value lightly all the homologies by which the comparative anatomists have built up their conceptions of relationship.

Evidence that hybridism has something to do with variation and hence with evolution was brought forward half a century before Lotsy—before Darwin and before Mendel. Lotsy's whole proposition is obviously a reaction to Mendelian thinking, but Mendel himself did not indulge in any such speculation. Rather, in the latter part of his paper he shows how the supposed transmutation of one type into

another through successive generations of hybrid stock is to be explained by the operation of the principles of heredity he had discovered.

Antedating Mendel's publication, however, is a paper by Naudin[3] on hybridism considered as a cause of variability. Naudin's work, unlike Mendel's, attracted such considerable attention at the time that it was translated in the newly established Journal of the Royal Horticultural Society. Naudin records what we now know as Mendelian segregation in the second generation of his hybrid plants, but failed to understand it. He also described hybrid vigor as regularly occurring in the first generation of his crosses and as disappearing in subsequent generations. He gave much experimental data, e.g. he made 130 hybrids of *Datura*. He recognized that reciprocal hybrids are identical, which was one of the great contributions of Mendel also. He believed that the variability of such genera as *Salix* was due to hybridity.

First-generation hybrids of *Datura ferax* × *laevis* were uniform and the reciprocal hybrids identical, but in the second generation "the most astonishing diversity succeeded the former great uniformity. . . . "I could bring forward many other examples of the excessive variability which arises in consequence of crossing."

He recorded striking hybrid vigor between *Mirabilis longiflora* × *jalapa*, whose progeny in the first generation "became enormous. Intermediate in the same degree between the parent species, which they far surpassed in stature, they resembled each other as exactly as possible, which might be expected as they belonged to the first generation." Of the second generation he said: "None of them acquired the large stature of the hybrids of the first generation; none, moreover, resembled them"—two were similar, the others very diverse.

More recently many writers have discussed hybridism as an evolutionary factor, and much controversy has developed as to the means of recognizing hybridity. Into this question it would not be appropriate to go in this place. The whole subject is in an incoherent amorphous stage. Doubtless, as more work is done, definite canons for research will crystallize out of the heterogeneous mass of facts and ideas floating around at present.

Meanwhile, further comparisons with other types of evolutionary theory may be useful.

[3] NAUDIN, CH. *On hybridism considered as a cause of variability in vegetables.* C. R. Nov. 21, 1864. Trans. Jour. Roy. Hort. Soc. 1(1). 1866.

Natural Selection drew a large part of its support from analogy with Artificial Selection, the process by which the extremely diverse types of domestic animals and cultivated plants (*cultigens*, as they have been called) were supposed to have originated. It was because of the importance of this analogy to his theory that Darwin devoted so large a part of his time to searching out the origin of domesticated types. It is a curious fact that in all the battle over Darwinism nobody questioned the efficacy of Artificial Selection. The validity of the analogy between breeds and species was vigorously attacked but not the origin of breeds. Agassiz said: "Selection is no doubt the essential principle on which the raising of breeds is founded and the subject of breeds is presented in its true light by Mr. Darwin."[4] Yet we know now that the origin of cultigens was one of the things least understood in Darwin's time. The present knowledge of cultigens was, indeed, one of the chief agencies in undermining Natural Selection.

It was on the same rock that DeVries' theory of mutation struck. It was later proved that the true-breeding *Oenothera* mutants which DeVries had found, sprang, not as he supposed, from a wild species, but from a cultigen which, as he discovered later very much to his chagrin, grows wild nowhere in the world. *Oenothera lamarckiana* is a hybrid which has been reproduced by crossing two wild species, *Oenothera biennis* and *O. franciscana*.[5]

In the hybrid origin of DeVries' oenotheras we have, naturally, a strong suggestion of the possibility of the hybrid origin of mutants in general and so of the whole of evolution. We will return to this. Meanwhile, we may take the other hint given us by DeVries' experience and examine cultigens more closely.

It is hardly too much to say that the origin of a majority of our staple food plants is as much a mystery as the origin of Orders and Familes. No man has ever seen growing in the wild, maize, bananas, sweet potatoes, cocoanuts, garden peas, tobacco, peanuts, lentils, or cassava. Neither has any wild species ever been discovered which, by such selection as Darwin relied on, could give rise to them.[6] No wild plant bearing anything even remotely similar to an ear of corn has been found after the most thorough search of the territory in which

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[4] AGASSIZ, L.   Am. Jour. Sci. **30**: 147.   1860.
[5] DAVIS, BRADLEY MORE.   *Oenothera neo-lamarckiana*.   Am. Nat. **50**: 688–696. 1916.
[6] The experiments of Johannsen (Ueber Erblichkeit in Populationen und in reinen Linien, Jena 1903) on garden beans and of many later workers on both plant and animal material have shown that within the limits of experimental experience, selection by itself is able to make practically no change whatever in an organism.

maize must have originated.[7] If we consider domestic animals, the case for nearly all of them, on Darwin's own showing, is nearly as bad.

There would be little profit for us here to go off into speculation as to the factors which have been at work in producing these old cultigens. But it may be worthwhile to look around among them for some whose origin is more recent and better authenticated.

Such are not to be found among the domestic animals or the staple crop plants of any people. All of these go back into the obscurity of antiquity, where they cannot be traced. But fortunately there is one type of cultigen which has been produced very recently and concerning which in some cases we have fairly detailed records. I refer to ornamental plants, nearly all of which have undergone great development within the past century.

Even among ornamentals of recent origin, recorded pedigrees of sufficient detail and accuracy for analysis are scarce. But wherever the facts have been obtainable the course of events has proved substantially the same.

In the beginning, nature lovers have dug up wild plants and grown them in gardens. Despite the belief entertained by Darwin and his contemporaries that domestication by and of itself in some mysterious way induced variability, many of these old species have been cultivated for centuries without undergoing much of any modification. Foxgloves and canterbury bells, geese and guinea fowl are very much as they were when first domesticated.

In contrast with such types others, like roses, dahlias, sheep, and dogs, show a diversity under domestication without parallel in the wild. When we search for the differences between the stable and the variable domesticated types, we find in every case where the facts are obtainable that hybridization has preceded the production of the polymorphic cultigens, while the stable types have no close relatives in domestication with which they could have been crossed.

A list of familiar cultigens which owe their character largely to hybridization includes azalea, begonia, calceolaria, cineraria, citrus, clematis, columbine, dahlia, delphinium, freesia, fuchsia, geranium (pelargonium), gladiolus, hibiscus, iris, ixia, peony, petunia, potato, rhododendron, rose, strawberry, sweet pea, tomato, tulip, verbena.

But polymorphic cultigens are not, for the most part, simple hybrids. Where their history can be made out the sequence of events has generally included three stages: (1) the collection of numerous wild

[7] KEMPTON, J. H.   *Maize, the plant breeding achievement of the American Indian,* Smithsonian Scientific Series. 11: 319–349.   1931.

species of a group; (2) a preliminary period of hybridization in which the results follow the ordinary expectations of Mendelian segregation and recombination; (3) what the horticulturists call a "break," when suddenly and all at once a large number of new forms burst forth unexpectedly as a result of further crossings. These breaks are entirely unpredictable in the light of our present knowledge and they have usually arisen in the gardens of practical men who could better preserve and disseminate the wonderful new varieties they had found than analyze the biology of what had occurred.

I doubt if anything could be more conducive to one's understanding of the processes of evolution than detailed consideration of the history of a cultigen in which such a "break" has occurred. There is no time here to go into the minutiae of the case, but I shall recount briefly the history of garden cannas.

Because of their luxuriant tropical foliage, cannas early attracted the attention of connoisseurs of exotics. A number of species were introduced from the wild during the first half of the nineteenth century. Bouché in 1833 grew in Berlin 37 of the 48 known species. The cultivation of these wild unimproved forms, however, died out soon after the middle of the century, and many of them have since been lost. An index of the interest in this line is afforded by the plates of Curtis' Botanical Magazine, which made a practice of figuring the novelties that were brought to British hothouses. Between 1787 and 1904 this serial gives 12 plates of cannas. All were before 1856 and all but two before 1825. During this early period nobody thought of growing cannas except as foliage plants in the greenhouse. Outdoor culture was a daring innovation, as witness the following comment by Seeman in 1855 on *C. warscewiczii*, from Central America, one of the three most important parents of present varieties (see Fig. 1):

In German gardens this canna is planted during the summer in open borders where it succeeds extremely well, as is also the case with other cannas, marantas, musas, begonias, bambusas, etc. In England this mode of culture has not yet been tried, probably from the prevailing notion that the difference of temperature of the two countries from May to October is too great to allow the experiment to succeed. There is no harm in trying it, especially as the case is not quite a hopeless one. The Germans formerly never dreamed that they should one day behold broad-leaved banana trees and cannas in their gardens flourishing with tropical luxuriance.[8]

The second period of canna culture centered about the work of Théodore Année who, enthused about cannas by a sojourn in South America, undertook to transform cannas from greenhouse curiosities

[8] Curtis' Bot. Mag., table 4854, June, 1855.

to outdoor plants. A good measure of his success is the fact that 20,000 clumps of his best variety, *C. annéei*, were planted in the public grounds of Paris in 1861.[9] His spirit was that of an amateur lover of fine flowers rather than that of a scientist or even a commercial horticulturist. Consequently we have very scanty records of the parentage of his varieties. And as all later work was based on his, this becomes an irretrievable gap in our knowledge of the evolution of garden cannas. Nevertheless, there are few even of ornamentals for which the deficiencies in our knowledge are not worse.
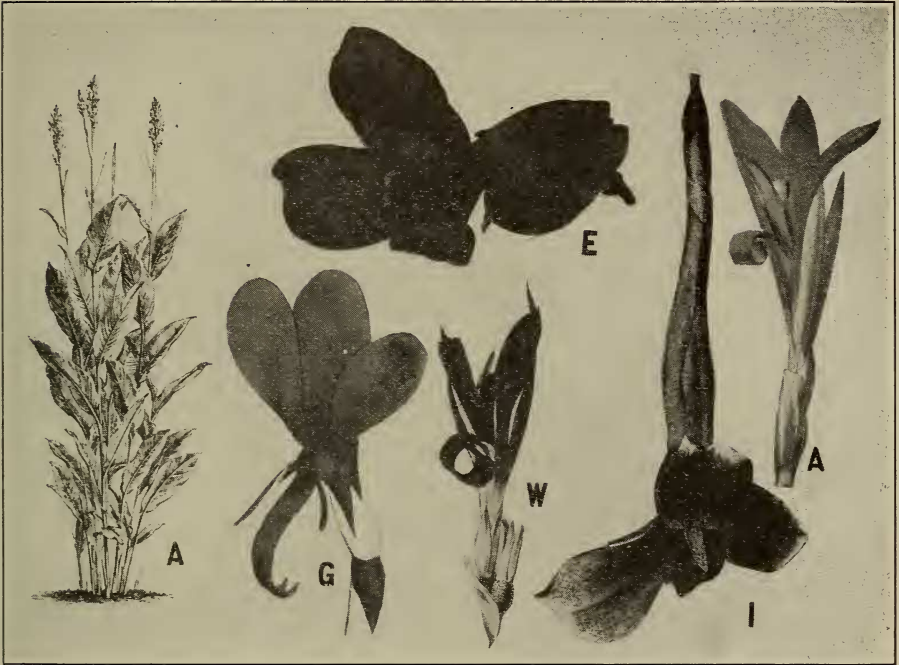

FIG. 1.—Ancestors of modern cannas—wild species and early hybrids. Flowers half natural size. A, *Canna annéei*, plant and flower. E, *C. ehemanni* (1 X W). Semipendent. G, *C. glauca*, source of the gene for yellow in cannas. I, *C. iridiflora*, pendent. W, *C. warscewiczii*, source of the gene for red in cannas. From the original figures. See text for citations.

Canna annéei was a lanky plant more than 13 feet tall with a few small salmon-pink flowers about the size of a snapdragon (Fig. 1). No one could imagine it being planted today, but it was a great favorite for several decades.

From the point of view of usefulness for further breeding and of beauty of its flowers the most noteworthy of the early hybrids was

[9] Rev. Hort., p. 469, 1861.

C. ehemanni, which is also attributed, though somewhat doubtfully, to Année. Positive and definite reports have it that this came from a cross of the small-flowered, brilliant red *C. warscewiczii*, alluded to above, and the pale, large-flowered *C. iridiflora* from Peru (Fig. 1).[10] It is probably safe to conclude that it sprang from the parents reputed, for no other plants known at the time could well have produced it. But it is doubtful whether it was a simple hybrid between these species. The cross was said to have been made by Année in 1863, but the hybrid plant was not described until 1875 and it seems unlikely that the finest canna of its time could have remained in obscurity for twelve years.[11] In view of its remarkable advance over either of its reputed parents, it is most unfortunate that we have no exact record of the time and place of its origin and of the name of the hybridizer.

While *Canna ehemanni* might be classed as intermediate between its parents, its flowers far surpassed either in effectiveness. They were nearly as large as the larger (*iridiflora*) and twice as numerous as the more floriferous (*warscewiczii*). The staminodes of *iridiflora* measured about 15 sq. cm., those of *warscewiczii* 2 sq. cm., and those of *ehemanni* 12 sq. cm. The number of flowers in *iridiflora* was about 6, in *warscewiczii* about 20, in *ehemanni* 40. Again, in color it was superior to either parent, for the deep scarlet of the petals had spread over the calyx, which had scarcely a trace of color in either parent.

The important thing to keep in mind with *Canna ehemanni* is its progress beyond anything known in the wild. The "break" was coming. In the next decade, that following 1880, the French breeders, of whom Antoine Crozy was the most celebrated, developed what were known as "gladiolus-flowered" cannas. This name, said a horticultural periodical[12] of the time "has been suggested for a remarkably beautiful class of cannas whose blossoms are almost as large and showy as those of the gladiolus."

The tradition concerning the origin of these gladiolus-flowered or French cannas was given in a letter by Henry L. de Vilmorin, one of the leading horticulturalists of his day, as follows: "It is the current belief in this country [*France*] and it seems confirmed by experiment that the new breed of floriferous cannas (i.e. the French dwarfs) originated by the crossing of *Canna ehemanni* with *C. warscewiczii* and with *C. glauca*[13] (see Fig. 1), the former producing red flowers and

[10] Rev. Hort. p. 111, 1861.
[11] Rev. Hort., pp. 291 and 321, 1875.
[12] Garden.   March 2, 1889.
[13] SMITH.   Exot. Fl.   **2**: t102.   1805.   *C. glauca* is an aquatic plant from the West Indies and South America.

the latter specially yellow-flowered varieties. Both original crosses intercross readily, and in later years I have had many crosses made every year and raised and named several dozen new seedlings using the best varieties of my own and Crozy's raising, without introducing new blood into the breed."[14]

Our credence of this straight-forward statement of "current belief" in the origin of French cannas must be modified by two circumstances: (1) Our knowledge that Année's early hybridization involving additional species had more to do with the foundation stock than Vilmorin realized. (2) From the species listed it is difficult to account for the numerous purple-leaved varieties of canna. This character, it would seem, must have come from *C. discolor*, which has such leaves. However, the flowers of that species (or perhaps it was itself a hybrid) have not had any discernible effect on modern cannas.

Turning now to a more detailed consideration of the methods used by the French breeders, we are told by the most famous of them, Antoine Crozy:

> As to the number of crosses raised by me, I suppose that I have raised without exaggeration some 180 to 200 varieties which, step by step, showed improvement over the older kind. Among my varieties not yet in commerce are cannas with flowers measuring from $4\frac{1}{2}$ to 6 inches in diameter. These have all very glowing colors and bear immense flower trusses.
>
> My constant zeal for superior varieties shows successes every year in regard to color as well as size and number of flowers. The flowers now are borne more erect, are of better substance, and show broader, rounder petals, and some are of a size not known before.[15]

Examination of Crozy's catalogs shows that his claim of 180–200 varieties is not an exaggeration but an understatement. I have not been able to lay hands on the full series of catalogs, but among those available an even 200 novelties are listed as produced by himself before the date of his statement. It is clear from the literature that in the production of cannas, once the right foundation stock was obtained, there was very little artificial selection of the sort hypothecated by Darwin. Though Crozy says he threw away many inferior sorts, rejection of culls played a very small rôle.

Rejection likewise was of no importance in the next great step in the improvement of the canna. Sprenger,[16] who originated modern or "orchid flowered" cannas, fertilized the flower of the most celebrated of the French cannas, Madame Crozy (Fig. 2), with pollen

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[14] In a letter published by F. A. Waugh in the Tenth Ann. Rept. Vermont Expt. Station.

[15] Gard. Chron.   Ser. III **21**: 362.   1897.

[16] SPRENGER, CHAS.   Rev. Hort., p. 85, 1896.

from the wild *Canna flaccida*. There was produced only one pod with three seeds, each of which gave rise to a new variety with flowers of a size previously undreamed of. The average staminode in these flowers attained an area of about 27 sq. cm. as compared with 9 sq. cm. in one parent and 7 in the other.
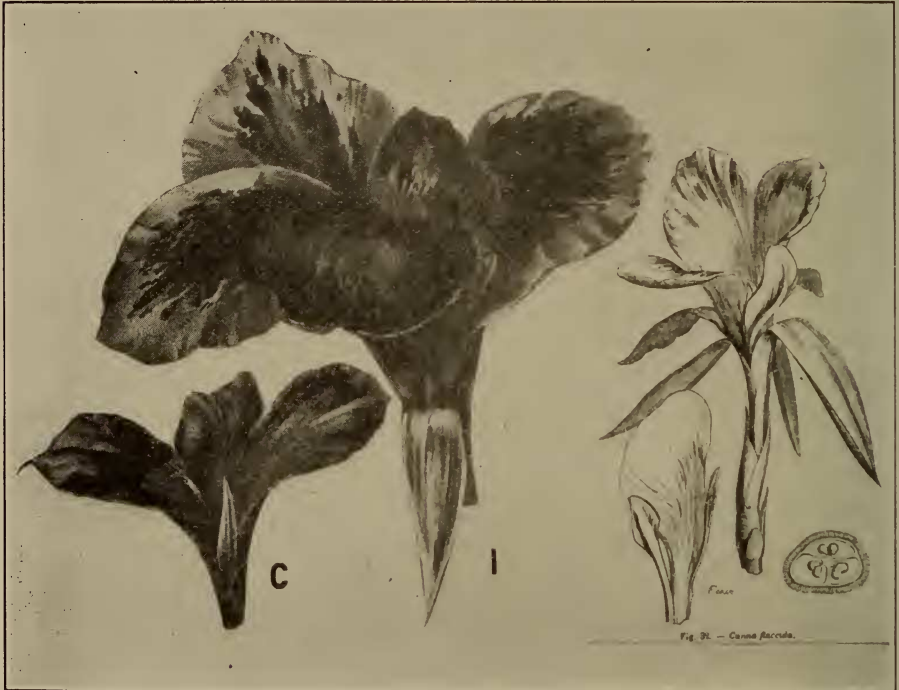

Fig. 2.—The first modern canna and its parents. Half natural size. C, Canna Madame Crozy (a complex hybrid involving the stocks shown in Fig. 1). I, *Canna italia.* F, *Canna flaccida*, native to Southeastern U.S.A. From the original figures.

Further testimony as to the small rôle played by rejection in plant improvement comes from Marion Shull, who relates (oral communication) the following experience with a cross between the iris varieties King and Julia Marlowe. A single pod with 8 seeds was obtained. Three of the plants from these received honorable mention among the novelties sponsored by the American Iris Society. Two more, though very fine varieties, were not sufficiently distinctive for exhibition, yet have been kept in the garden ever since for his own enjoyment. A sixth was practically identical with one of the parents, leaving only two to be rejected, and Shull adds that these were better than many of the "choice" varieties commonly grown. To one who supposes that selection on a large scale is a necessary part of plant

improvement, a visit to Shull's garden is highly instructive. There, on a little plot of ground about 50×50 feet, have been originated probably more superior varieties of iris than in any other garden, and yet more ground is given over to the multiplication of old varieties than to the production of new ones, and a large fraction of the space is occupied by other plants grown entirely for ornament. Further, the rejects that are culled out are nearly all thrown away because they are not sufficiently different from older types rather than because they are inferior.

The most important feature of the origin of cultigens through hybridization is its progressive character, which is recognized by all breeders. The new forms cannot be interpreted at all as due to recombinations of characters already present. There is an emergence of new characters previously considered impossible. In the light of what has since occurred the following rebuke by André, the experienced editor of Revue Horticole, 1866, to the enthusiasm of Sisley, who encouraged by a preliminary success, dared predict cannas with flowers "as big as gladioli" is significant as well as amusing. He says that while he fully appreciates the marvelous improvements made by breeding, "the cannas already obtained clearly reveal the limit which we may not pass beyond—it is not possible to nourish the hope of those famous cannas with flowers like gladioli on which M. Année counted formerly but no more."[17] To appreciate the force of this opinion one must remember that it was written before even *C. ehemanni* was known.

The nature of the "breaks" by which cultigens rise out of the apparent limitations of their ancestry into new classes of utility in size or productiveness is not at all adequately understood. In some cases they are due to the incidence of polyploidy, as discussed below. The phenomenon of the break can be expressed in the terminology of genetics[18] by using the conception of latent genes. To speak of a latent gene does, however, little more than name a phenomenon which is as mysterious as ever. Yet it might perhaps provide a point of view from which experimentation could start.

In the light of our present knowledge of cultigens, then, it begins to appear possible once more that Darwin was right in supposing that the improvement of domestic plants and animals was the key to the origin of species.

Meanwhile, there are some other phenomena more or less con-

[17] Gard. Chron., p. 537, 1866.
[18] R. K. Nabors. *Emergent evolution and hybridism.* Science **71**: 371–375. 1930.